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THE CLASSIFICATION OF PLANTS, IX.*

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Our knowledge of the gymnosperms has been greatly advanced in recent years and it is now possible to discern the broad, general lines of relationship among them with some degree of certainty. Especially important have been the contributions on the morphology of the cycads and various conifers by Chamberlain and other Chicago botainists.

In some orders, the phylogenetic relationships are still uncertain and much work remains to be done both on the cytology and on the histology of the stem. In certain genera even the gross organography is not completely known. Among the conifers, the Podocarpaceæ and certain Taxodiaceæ greatly need serious attention.

The recent discoveries in the Pteridospermae and other fossil groups and the finding of multiciliate, motile sperms in the living Cycadophyta have definitely related the Gymnosperms to the Ptenophyte phylum; and, although one would hardly look to any known living Gymnosperms as direct ancestors of the Angiosperms, yet it seems certain that the Angiosperms and the various groups of Gymnosperms must have had rather closely related ancestors derived directly from the eusporangiate ferns. There is little probability that the real ancestry will ever be discovered, at least not until more progress is made in finding plant remains or impressions of far earlier times than any yet known. The fossil history of plants practically begins with the Cordaites, and although one may find interesting transition forms between

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the various members of primitive seed plants in the Carboniferous and Devonian, the conclusions drawn from these sources are no more reliable or fundimental than those from living forms, except that they aid in filling up gaps which occur among those surviving to the present time.

What is needed, of course, is a series of ancestral fossils below the Devonian, leading up step by step through the successive geological formations, from a pteridophyte ancestor to the Devonian Cordiates. The speculations of those who reason from fossils of lower order which occur after the higher have appeared are of no more weight than speculations based on the present flora, which is, after all, more reliable than the extremely fragmentary material of the fossil record. It may be stated that there are, at present, no evident data in support of the direct relationship of any gymnosperm classes unless we consider the Bennettilales as a class distinct from the Cycadales. The relationship of these two groups seems to be quite certainly established. But at present most systematists would probably agree that the Cycadales and Bennettilales are closely related orders.

The strobili or cones of the Coniferæ are here regarded as true strobili and not as inflorescences, and Bessey's view that the staminate and ovulate cones are strictly homologous is maintained. When one compares the pine carpel, with its prominent ovuliferous scale, with the dwarf branch, one might easily be tempted to make them homologous; but when one goes a little further and finds the same peculiarities in the carpels of genera like Abies, where no dwarf branches exist, the conclusion has little or no weight. Much of the discussion as to the nature of the carpellate strobilus of the Pinaceæ has been based on the occurrence of occasional abnormal structures, but one can find abnormal cones that argue for the view that the carpellate cones are true strobili and not inflorescences, just as well as one can find structures that would indicate the opposite. For example, Fischer has described an abnormal cone of Pinus laricio, the lower part of which had normal stamens and the outer end of the same axis had carpels of the usual type. This bisporangiate cone was in the position of a staminate cone beside a normal staminate cone. The carpels had the usual carpellate bract and ovuliferous scale. I regard the ovuliferous scale as a peculiar structure not homologous to either stem or leaf. The fleshy structures in the Taxales must be of a similar nature. The aril of Taxus, for example, is either homologous or analogous to the ovuliferous scales of Abies and Picea.

The structure with the two ovules in Ginkgo is regarded as a megasporophyll, the whole cluster at the tip of the dwarf branch being simply a cluster of carpels. The same interpretation must then, of course, also be given to the staminate structures. The stalk with its numerous anthers being a compound microsporophyll homologous to those of the Bennitales and the cycads. On the other hand, the sporebearing structures of the Gneteae are regarded as highly specialized strobili, the whole cluster being an inflorescence. If these views are correct, we have in a general way the same evolutionary developments in the gymnosperms as are so evident in the angiosperms. There are, however, no great number of transition types as we have in the angiosperms, where one can follow through from the primitive strobilus-like flower to a highly reduced and specialized inflorescence, with numerous vestiges, pointing out the probable course of evolution.

The arguments usually advanced from the presence of abnormalities, as stated above, are far from convincing. The change of one organ to another, or the appearance of a structure peculiar to one organ on another, simply mean that the hereditary factors have become active in a tissue where they are normally inactive or latent. One would certainly not claim that when the stamen of a rose or other flower is transformed into a petal there is a revision to a primitive condition. For this would give us a primitive flower composed entirely of petals. It is evident however, that the evolution of the rose and all other similar flowers must have proceeded in the opposite direction. Instead of a reversion we have in such cases only the expression of resident factors in structures where we do not expect them to be operative. The petal factors are present, potentially, in every cell of the entire plant body.

Because a petiole under an abnormal stimulus, caused by certain bacteria or by special manipulation, may develop stem structures is no evidence that the petiole was phylogentically ever a stem. If one finds stem-like tissues in the carpel petiole of Ginkgo, there is no unquestionable evidence that the organ was phylogenetically a stem. The stem structure may have developed as a response to the parasitism of the gametophyte and its embryo. It is also true that in the great majority of supposed phylogenetic reversions, there are after all no hereditary characters shown in the abnormal structure but what appear in the normal ontogeny. Usually there is simply an abnormal distribution in the expression of such characters. If a root under an unusual manipulation can give rise to tissues which produce flowers, this does not mean that in its past phylogeny the root was a petaliferous organ. Yet such interpretations are continually made by some biologists to account for any abnormal developments which may be shown in the various tissues of organisms.

One could certainly reconstruct a remarkably fantastic ancestral group of angiosperms or gymnosperms, were one to give weight to the multitude of monstrosities continually appearing in both vegetative and reproductive parts.

With the foregoing views as a basis for our reasoning on the phylogemy of the gymnosperms, we may regard the hypothetical relationships of the various classes and other groups as follows:

The Pteridospermae were a class of fern-like seed plants, derived from a heterosporous ptenophyte group, not yet discovered, leading off from some primitive eusporangiate, homosporous type long before Devonian times. These homosporous ferns must have had characters somewhat like our living Marattiales.

The Cycadeae are a more highly specialized branch, derived from the same primitive stock as the Pteridospermae. The Strobilophyta must also have been derived from the ancestral type which gave rise to the Cycadeae and Cordaiteae, but did not originate directly from either group. There is no satisfactory evidence that the Coniferae came from the Cordaiteae, but the two groups may have had a common ancestry segregated from some primitive Pteridosperm stock.

The Ginkgoeae seem to connect directly with the Cordaitales, but the latter are still too imperfectly known to make a comparison certain. As to the origin of the Geneteae, there is little evidence They must have been segregated in very ancient times from the early Strobilophyta, probably before the various groups composing the phylum had received their present distinguishing characters. They may have been segregated from the Strobilophyte phylum soon after the Anthophyta had been segregated from the same primitive stock as the typical Strobilophyta.

The Anthophyte phylum must have been separated long before it had advanced to its present unique morphology; perhaps at the very beginning of its seed bearing habit. The enlarged vessel-like tracheids of the Gneteae and other supposedly angiosperm characters must be regarded as merely analogous developments and not as indicating a direct line of ancestry for the Anthophyta.

The synopsis of the living Gymnospermae follows below, being carried out as far as the ordinarily recognized genera. Some of the families, as for instance the Pinaceae, present a very striking series of progressive developments and specializations. This is shown in the specialization of the leaves, dwarf branches, ovuliferous scales, carpellate bracts and other structures.

Beginning with such forms as Araucaria imbricata, as approaching the more primitive organography, and then passing through the Pinaceae, one finds a progressive tendency which finds its highest expression in Pinus. In the genus Pinus one can again find a considerable range of advancement. In Araucaria imbricata there is but one type of leaves and one type of branch; in Pinus there are four kinds of leaves and two kinds of branches and the dwarf branches are specialized to the extreme limit. The carpel also shows successive degrees of specialization. The cones and ovuliferous scales of the white pines show an intermediate type of development between those of the spruce and Douglas-fir on the one hand and the more specialized two-leaved pines on the other.

By some, relationships and phylogenies are interpreted mainly through supposed similarities of the vascular structures. Such classifications are, however, vain unless they are supported by the combined evidence of all other structures, at least until it can be shown that the extremely hypothetical assumptions used as a basis for interpretation can be established with some degree of probability. There are no primitive vascular plants known, as indicated above, which might be used as a basis of comparison. The fossil record is a blank for any plants which would lead us to the beginning of vascular evolution and the lowest living Homosporous Pterdophytes show a considerable diversity. The living homosporous classes are about on a general level of evolutionary development and the assumption that the protostele or any other type of vascular structure is the most primitive remains to be proven. There is also no evidence that the vascular system or any other stem structure is less subject to modification than are leaf, root or reproductive structures, none of which have escaped changes of a profound nature. The assumptions based on the embryogeny of the vascular structures are no more certain than those based on the embryogeny of the reproductive parts. Nevertheless, the careful study of the vascular systems will give us another important aid in deciphering the true relationships of the higher plants, provided that the knowledge gained is correlated with evidence from other lines of investigation. It is, no doubt, permissable to call supposed embryonic recapitulations to our aid in attempting to reconstruct the hazy course of phylogenetic history, but it must be regarded as only one of the lines of evidence to be considered along with every other clue one may obtain from every structure, function, and peculiarity of the plant in its entire life cycle.

Synopsis of the Cycadophyta.

I. Leaves compound; stem an unbranched shaft or with few branches.
   1. Megasporophylls only slightly differentiated from the foliage leaves; leaves fernlike, often very much compounded; no cones formed. (Fossil). PTERIDOSPERMÆ.
   2. Megasporophylls highly specialized, usually very different in form from the foliage leaves; in Cycas still showing some foliage characteristics; leaves pinnate, rarely bipinnate; at least one kind of sporophylls in cones. CYCADEÆ.
      a. Microsporophylls leaflike; flowers probably all bisporangiate. (Fossil). **BENNETTITALES.**
      b. Microsporophylls not leaflike, arranged in compact monosporangiate cones; diecious. **CYCADALES.**

II. Leaves simple or merely lobed, venation dichotomous or parallel; stems with numerous branches forming a dense crown.
  1. Without dwarf branches; leaves usually elongated, with parallel veins. (Fossil.) CORDAITEÆ **CORDAITALES.**
  2. With thick wart-like dwarf branches; leaves fan-shaped, entire or lobed, sometimes deeply divided, deciduous.
    GINKGOEÆ. **GINKGOALES.** GINKGOACEÆ. **Ginkgo.** Maiden-hair-tree.

SYNOPSIS OF THE CYCADALES.

I. Megasporophylls (carpels) leaf-like, arranged in a rosette through which the main stem continues its growth; seeds 8—4, seldom 2, horizontal or erect; leaflets with a midrib; cortical cauline vascular bundles present. CYCADACEÆ. **Cycas.**
II. Megasporophylls (carpels) highly specialized, arranged in lateral cones; seeds 2, inverted; pinnæ parallel-or feather-veined. ZAMIACEÆ.
  1. Cortical cauline vascular bundles present, forming several wood zones. MACROZAMIATÆ.
    (1). Leaves simply pinnate.
      a. Carpels pointed. **Macrozamia.**
      b. Carpels shield-shaped. **Encephalartos.**
    (2). Leaves doubly pinnate; stem subterranean. **Bowenia.**
  2. Cortical bundles absent; primary cambium persistent. ZAMIATÆ.
    (1). Leaflets feather-veined. **Stangeria.**
    (2). Leaflets parallel-veined.
      a. Ovules on a process of the carpel; carpel pointed and leaf-like. **Dioon.**
      b. Ovules sessile; carpels shield-like.
        (a). Carpels shield-like, not horned.
          ((a)). Tree-like when mature; carpellate cones 2–3 ft. long. **Microzamia.**
          ((b)). Usually with a low tuberous stem or geophilous; carpellate cones much smaller. **Zamia**
        (b). Carpels 2-horned. **Ceratozamia.**

SYNOPSIS OF THE STROBILOPHYTA.

I. No vessels (enlarged tracheids) in the secondary wood; wood frequently with resin ducts; cotyledons 2–15. CONIFERÆ.
  1. Carpels usually numerous, in strobili (cones); seeds covered by the carpel tips or by ovuliferous scales; cones rarely becoming fleshy when mature; seeds dry, the testa woody or leathery. **PINALES.**
    (1). Leaves spirally arranged.
      a. Pollen wingless; carpels with one to several seeds; ovuliferous scale not prominent, or none.
        (a). Carpel with one seed; microsporangia 5–8, free and pendulous. ARAUCARIACEÆ.
        (b). Carpel with two to nine seeds; microsporangia 2–5. TAXODIACEÆ.
      b. Pollen grains winged; carpels with two inverted seeds; ovuliferous scales prominent; plants monecious. PINACEÆ.
    (2). Leaves opposite or whorled. JUNIPERACEÆ.
  2. Carpels of the cone few or 1; seeds with fleshy testa or covered by a fleshy aril. **TAXALES.**
    (1). Stamens with 2 microsporangia; pollen winged; seed 1.
      a. Not with phylloclades. PODOCARPACEÆ.
      b. With phylloclades. PHYLLOCLADACEÆ. **Phyllocladus.**
    (2). Stamens with 3–8 microsporangia, seeds 1 or 2, erect, pollen wingless. TAXACEÆ.

II. Vessels present in the secondary wood; wood without resin ducts; embryo with 2 cotyledons; strobili in specialized inflorescences; leaves opposite. GNETEÆ.

1. Archegonia well developed; primary cambium persistent; leaves scale-like; stem green and fluted.
EPHEDRALES. EPHEDRACEÆ. **Ephedra.**

2. Archegonia reduced; concentric cortical series of vascular bundles produced; leaves ribbon-like or broad. **GNETALES.**
   a. Leaves only 2, ribbon-like and split when old; stem tuberous. TUMBOACEÆ. **Tumboa** (Welwitschia).
   b. Leaves numerous, broad, netted-veined.
GNETACEÆ. **Gnetum.**

SYNOPSIS OF THE FAMILIES OF CONIFERÆ WITH MORE THAN ONE GENUS.

ARAUCARIACEÆ.

1. Seed without a wing, coalesced with the carpel. **Araucaria.**
2. Seed winged, free from the carpel. **Agathis.**

TAXODIACEÆ.

I. Dwarf branches; if any, and the leaves not all deciduous at the same time.
1. Not with true dwarf branches.
   (1). Ovules or seeds 3; carpellate cones often clustered at the end of the twig; leaves rather broad. **Cunninghamia.**
   (2). Ovules or seeds, 2, or more than 3, if 3 then the carpellate bract toothed; leaves rather narrow or scale-like.
      a. Microsporangia on the stamen 3–6.
         (a). Carpellate bract not toothed.
            ((a)). Seeds 2; carpellate cones ½ in. long. **Taiwania.**
            ((b)). Seeds 4–9; carpellate cones 1 in. or more in length. **Sequoia.**
         (b). Carpellate bract toothed; seeds 3–6. **Cryptomeria.**
      b. Microsporangia on the stamen 2; carpel with 4–9, mostly 5 seeds. **Arthrotaxis.**
2. Dwarf branches extending into a long double needle; microsporangia 2, seeds about 7. **Sciadopytis.**

II. Dwarf branches deciduous; carpel shield-like, ovules 2.
1. Ripe carpels persistent. **Taxodium.** Bald-cypress.
2. Ripe carpels deciduous. **Glyptostrobus.**

PINACEÆ.

I. Without dwarf branches.
1. With sterigmata; carpels persistent.
   (1). Carpellate bracts longer than the ovuliferous scales; leaves flat. **Pseudotsuga.** Douglas-fir.
   (2). Carpellate bracts shorter than the ovuliferous scales.
      a. Leaves prismatic, carpellate cones drooping. **Picea.** Spruce.
      b. Leaves flat.
         (a). Carpellate cones drooping. **Tsuga.** Hemlock.
         (b). Carpellate cones erect. **Keteleeria.**
2. Without sterigmata, carpels deciduous; carpellate cones erect; carpellate bract longer than the ovuliferous scale; leaves mostly flat. **Abies.** Fir.

II. With dwarf branches.

1. Dwarf branches persistent; leaves numerous, ordinary branches also with leaves.
   (1). Leaves evergreen. **Cedrus.** Cedar.
   (2). Leaves deciduous each year.
      a. Carpels persistent. **Larix.** Larch.
      b. Carpels deciduous. **Pseudolarix.** False Larch.
2. Dwarf branches deciduous (self-pruned); leaves few; ordinary branches with scale leaves only. **Pinus** Pine.

JUNIPERACEÆ.

1. Cones woody, at the ends of ordinary leafy branches. CUPRESSATÆ.
   (1). Carpels imbricate, not shield-shaped.
      a. Carpels with 4–5 seeds. **Thujopsis.**
      b. Carpels with 1–3 (usually 2) seeds.
         (a). Carpels 6–8, the four upper fertile. **Thuja.** Arborvitæ.
         (b). Carpels 4–6, the two upper fertile. **Libocedrus.**
   (2). Carpels valvate, not shield-shaped.
      a. Carpellate cones with numerous sterile bracts at the base. **Actinostrobus.**
      b. Carpellate cones with the upper set of carpels seed-bearing, the lower sterile. **Fitzroya.**
      c. Carpellate cones with 4 carpels, without sterile bracts at the base. **Callitris** (including Widdringtonia).
   (3). Carpels shield-shaped.
      a. Carpels with several seeds. **Cupressus.** Cypress.
      b. Carpels with 2 seeds. **Chamæcyparis.** White-cedar.
2. Cones fleshy when mature, at the ends of short or axillary branches. JUNIPERATÆ. **Juniperus.** Juniper.

PODOCARPACEÆ.

1. Seed more or less inverted, at least in the incipient stage.
   (1). Both stamens and carpels in definite cones.
      a. Leaves flat, needle-shaped; carpels spirally arranged; monecious. **Saxegothæa.**
      b. Leaves opposite, scale-like appressed; carpels in whorls of 4; diecious. **Microcachrys.**
   (2). Carpels 1 or few, not in a definite cone.
      a. Seed completely inverted, all the parts of the carpel grown together. **Podocarpus.**
      b. Seed only partly inverted, outer bract of the carpel not united with the seed. **Dacrydium.**
2. Seed erect; leaves scale-like; shrubs. **Pherosphæra.**

TAXACEÆ.

1. Carpel with 2 ovules. **Cephalotaxus.**
2. Carpel reduced, ovule 1.
   a. Carpellate flowers two together; seed closely invested by the outer fleshy layer; matured female gametophyte grooved. **Torreya.**
   b. Carpellate flowers usually solitary; seed surrounded by a free aril; matured female gametophyte even. **Taxus.** Yew.